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THE EVOLUTION OF THE MAMMALIAN MIDDLE AND OUTER EARS: A PERSONAL REVIEW

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I. INTRODUCTION

The comparative anatomy of the vertebrates (including the comparative embryology and vertebrate palaeontology) has much to offer zoologists because it is here that we see best the actual transformation of organs into homologous but vastly different structures which function quite differently. We have the possibility also of understanding how animals can so change that the evolutionary results are separated into different classes.

The description in the middle of the last century by Owen of the first discovered mammal-like reptiles did not arouse great interest, perhaps because much of the material was of indifferent quality and the techniques then available for their preparation and study were primitive when compared with those available today. It was the visit paid by Seeley to South Africa later in the century, and particularly his accounts of such cynodonts as *Cynognathus ceratinotus*, which aroused serious interest. One result of this was that Broom migrated to South Africa and during the next half century described hundreds of specimens collected from the Permo-Triassic Karroo fauna, the majority of which were synapsid, or mammal-like, reptiles. Later Watson's accounts (1911, 1913) of the cynodont *Diademodon* attempted for the first time to interpret the real nature of, and to some extent, the mode of life of these animals. His account of the lower jaws of cynodonts, drawing attention to the reduced postdentary bones, caused Palmer (1913) to compare them with the ear bones of an embryo marsupial. The resemblance was such as to establish finally Reichert's long famous theory, based entirely on living animals, that the mammalian malleus, incus and stapes were the homologues of the reptilian articular, quadrate and columella auris. But Palmer's comparison also showed that the mammalian tympanic bone was unquestion-

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ably derived from the reptilian angular bone with its reflected lamina. This was the position when I began studying cynodonts in the early thirties. I had collected my first cynodonts in South Africa in 1930 and collected more of them, and other theriodonts, in 1933 in both East and South Africa. During these years I became convinced that the urgent need was to produce the finest possible preparations from the best available material. This view I owed to Stensiö whose account of the fossil Agnatha (Stensiö, 1927) startled the world of zoologists. I visited his laboratories in 1931 to study his superb equipment and to admire the patience with which he devoted years of technological work and study to one small specimen. No pains, I felt, should be spared to obtain accurate information on synapsid reptiles where this was possible. Today specimens and techniques are available of a quality almost unknown to such workers as Broom and Watson. Examination of material used to establish types and theories in the last century will convince most palaeontologists of the truth of what I have written. An example of the difficulties I met can be seen in Broom's (1932) book. There in his fig. 90F Broom showed the reflected lamina of the angular bone of *Thrinaxodon liorhinus* as a broad sheet of bone which covered nearly all the post-dentary bones laterally, leaving no room for a tympanum of the sort supposed by Watson to exist in later cynodonts. But, on the same page, Broom figured a new species of *Thrinaxodon*, *T. putterilli*, and here the reflected lamina was slender and curved, greatly resembling the tympanic bone of some primitive mammals. This great difference was not even mentioned in the text and when in 1933 I asked Broom where the type was he was unable to tell me. Later I was able to examine a specimen which I thought showed the lamina much as in Broom's *T. liorhinus*, and I figured it so (1946). If anyone cares to study the astonishing position we have now reached in this matter they should compare the illustrations of this reflected lamina published by Crompton (1963), Barghusen (1968; fig. 8*c*) and those of Allin (1975) (Fig. 1). How far the differing shapes and sizes are due to imperfections; how far they may represent different growth stages; and how far they may be natural variations it is impossible for anyone to say unless they have had access to the original specimens. But imperfect preservation and preparation probably accounts for much, and calls attention to the need of more and accurate facts (see Van Heerden, 1972).

In my earliest papers I expressed doubts about the theory which equated the reptilian parasphenoid with the mammalian vomer (Parrington, 1933, 1935) and wished to discuss the matter with Broom. However, he replied that the matter had been settled in the last century and turned to other matters. Some years later Westoll told me that he was sure I was right and asked why I did not publish the matter at length. As nobody had paid any attention to my brief papers I asked him whether they would do so if I published at length. His reply was, in effect "Yes, they would." I then pointed out what seemed to me to be a muddle about the pterygoids and we agreed to work together on the whole story of the evolution of the mammalian palate, using the data from comparative anatomy, comparative embryology and palaeontology, starting with the condition in the crossopterygian fishes and following it through primitive tetrapods, and pelycosaurs and the theriodonts. The result of this work (Parrington & Westoll, 1940) has never been challenged in print as far as I know. While this work

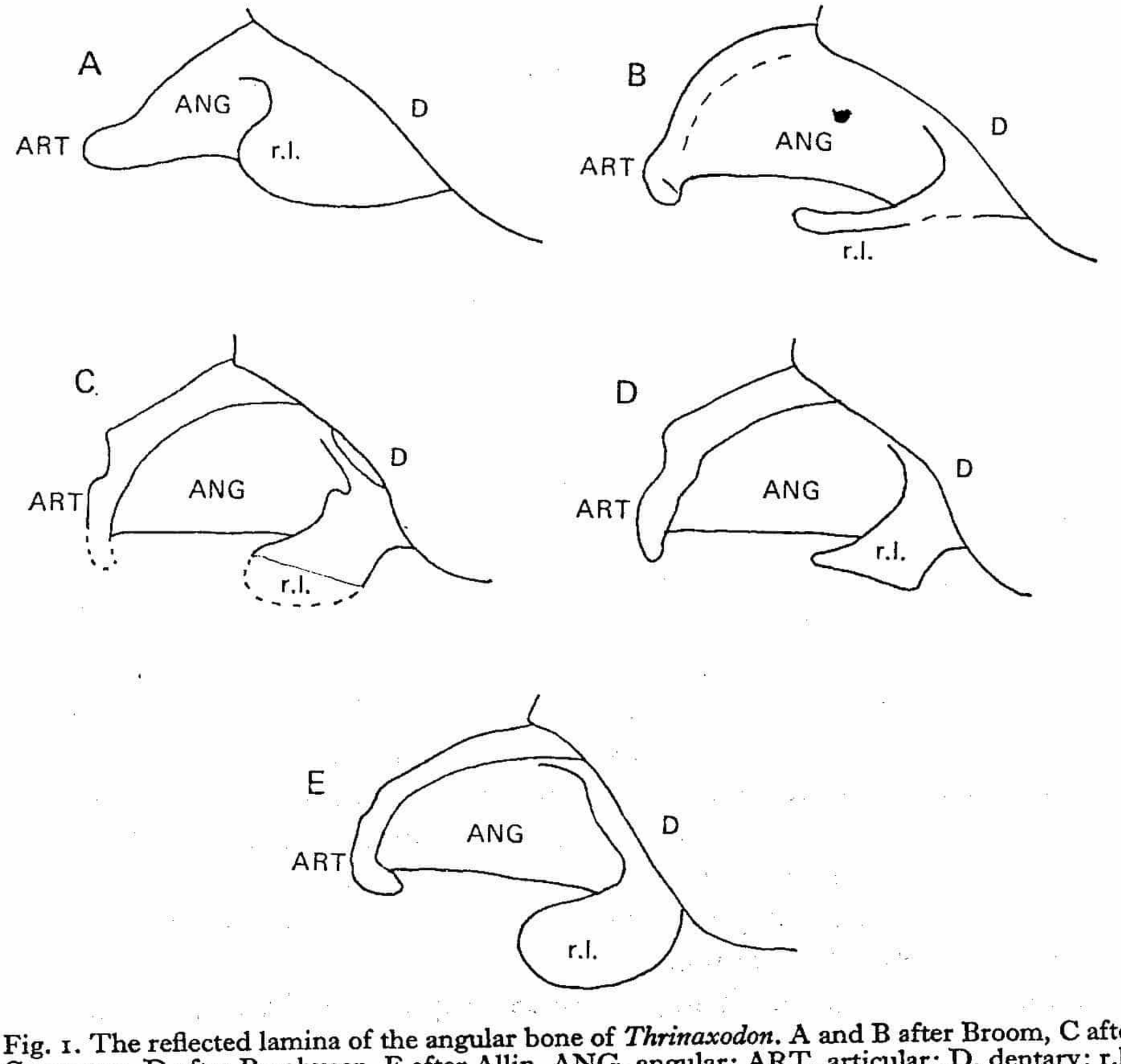


Fig. 1. The reflected lamina of the angular bone of *Thrinaxodon*. A and B after Broom, C after Crompton, D after Barghusen, E after Allin. ANG, angular; ART, articular; D, dentary; r.l., reflected lamina.

was being carried out I pointed out to Westoll the difficulties of the current views on the cynodont middle ear and we agreed to work together on that, in a similar comprehensive manner. However the war intervened and the work was never carried out.

II. WESTOLL'S THEORY

When I returned to Cambridge in 1945 there was much to be done. Six years reading was waiting for me; most of the work for a paper on cynodonts had been done while studying them for the paper on the evolution on the mammalian palate; and a collection of mammalian teeth from the Upper Trias awaited study and description.

Several of the papers waiting for me were of special interest. Romer & Price (1940) had shown in their magnificent monograph on the pelycosaurs that only the sphenacodonts had a reflected lamina of the angular (Watson believed that all pelycosaurs had this structure) and that in these a tympanum held by the lamina could not be connected to the stapes by any reasonable extra-stapes. The second publication was one by Westoll (1943) which was followed by two shorter ones (1944, 1945). These

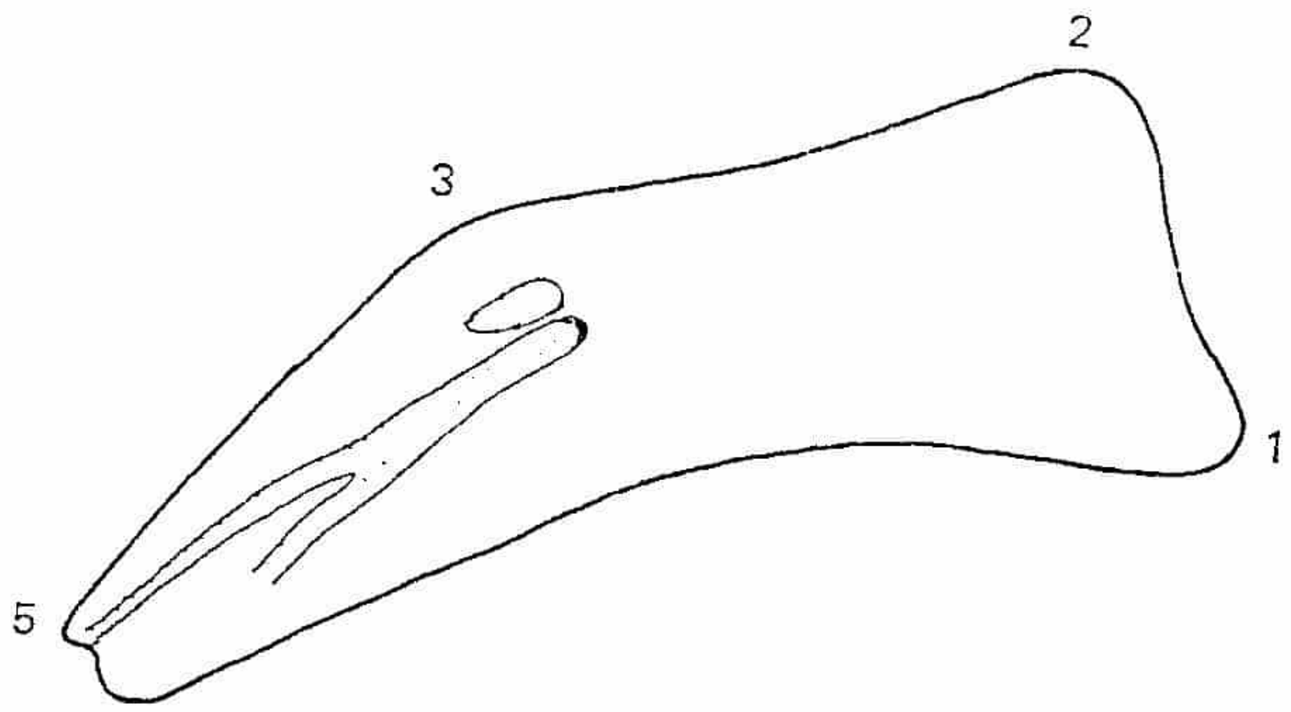


Fig. 2. Sketch of the right hyomandibular of *Eusthenopteron* (outer aspect). 1, processus ventralis; 2, processus dorsalis (these two are more clearly separated in internal aspect); 3, opercular process; 4, processus quadratus; 5, position of attachment to the remainder of the hyoid arch. The canal carried part of the facial (VII) nerve. (Data from Westoll.)

advanced a theory on the evolution of the mammalian middle ear. Using comparative anatomy, embryology and what was then known of the palaeontology of the relevant animals he claimed that the hyomandibular bone of crossopterygian fishes had various contacts or processes for attachment, and that these could be equated with processes or points of attachment in many stapes of living animals and, sometimes, in fossil forms. I found Westoll's theory very plausible but I knew that in some cases I could check the theory by examining material from the Permian and Trias of Africa. The result of doing so was illuminating.

In essence Westoll's theory held that the crossopterygian hyomandibular had five processes, or points of contact, and that these could often be traced in tetrapods. These five points were: (1) the processus ventralis which became the footplate of the stapes of tetrapods, inserted into the fenestra ovalis; (2) the crossopterygian processus dorsalis which became the tetrapod dorsal process; (3) the opercular process which became the tetrapod extra-stapes; (4) the crossopterygian processus quadratus which became the connection to the quadrate boss in labyrinthodonts or of contact in amniotes; and (5) the attachment to the hyoid bone which was a formal requirement of comparative anatomy and could reasonably be supposed to have existed at least in the young (Fig. 2). These have been tabulated (Parrington, 1955, p. 36).

Moreover Westoll's suggestion that the reptilian tympanum became the *pars flaccida* when the mammalian tympanum came into being seemed very satisfactory, though this was later challenged by Shute (1956) who claimed that the course of a branch of the facial nerve, the chorda tympani, did not conform.

Since this account was first submitted for publication Lombard & Bolt (1979) have published a substantial paper discussing the evolution of tetrapod ears. They follow Allin (1975) which, it will be seen, I am unable to do. They lay special emphasis on the relations of the internal mandibular branch of the facial nerve (chorda tympani). They report that the nerve has the same relations to the stapes in all tetrapods except salamanders and gallinaceous birds. If its relations can vary within the

birds, is it a reliable guide elsewhere? Their conclusions state that the tympanic membranes of all recent tetrapod classes are independently derived. It seems to me that Occam's razor, or the economy of hypotheses, or, best of all perhaps, parsimony of assumptions, has been neglected.

III. THE PALAEONTOLOGICAL EVIDENCE SUPPORTING WESTOLL'S THEORY

One result of my work on the evolution of the mammalian palate was that it became possible to describe more accurately and in fuller detail the skull of the cynodont *Thrinaxodon liorhinus* from the Lower Trias of South Africa (Parrington, 1946). Clearly the preparation of one skull, which had not suffered crushing, was such as to invite detailed examination of the one stapes which had remained in place. A few hours work with a needle showed that, as was to be expected if Westoll's theory was correct, there was a slender dorsal process at the postero-distal end of the stapes. This process was perfectly formed medially, where the perichondral bone was continuous with that of the stapes itself, though distally the ossification faded into matrix as did the distal end of the stapes – it seemed quite clear that the end of the stapes and the outer part of the dorsal process were originally completed in cartilage. Such a cartilaginous end would allow the presence of a cartilaginous extra-stapes, as occurs in modern reptiles, and also an abutment against the quadrate and, embryologically at least, a connection with the rest of the hyoid arch. The tympanum would be supposed to lie behind the quadrate, as in reptiles generally, and at the end of the external auditory meatus. The presence of this dorsal process in *Thrinaxodon* was later confirmed by Estes (1961).

The examination of some Middle Triassic cynodonts from East Africa revealed two specimens, wrongly identified at the time as *Trirachodon* (see Crompton, 1955) which were very helpful. One specimen had the left stapes lying in the matrix between the basisphenoid–parasphenoid complex and the alisphenoid, i.e. within the cavum epipterycum. The specimen had a bony extension projecting from what I can only interpret as having been the postero-distal end. The length of the stapes itself about bridged the distance between the fenestra ovalis and the position where the median end of the quadrate condyle must be expected to have lain, though the quadrate itself was missing. The bony extension can only have been interpreted as an ossified extra-stapes which projected behind the quadrate condyle. Another specimen showed what appeared to be the end of the bony external auditory meatus, slightly dilated, lying behind the position where the missing quadrate must have been situated.

Allin (1975) has challenged this interpretation. He has seen a cast of the specimen showing the supposed extra-stapes and presents a sketch which, he claims, shows that the bone could not have lain as I interpreted it, being too long.

Soon after the accounts of the two specimens were published, Watson, who had long studied cynodonts, visited Cambridge. He took a pair of dividers and, first setting them to the length of the main body of the stapes, placed one end into the fenestra ovalis and then satisfied himself that the distal end of the bone would reach about the position where the medial end of the quadrate condyle would have lain.

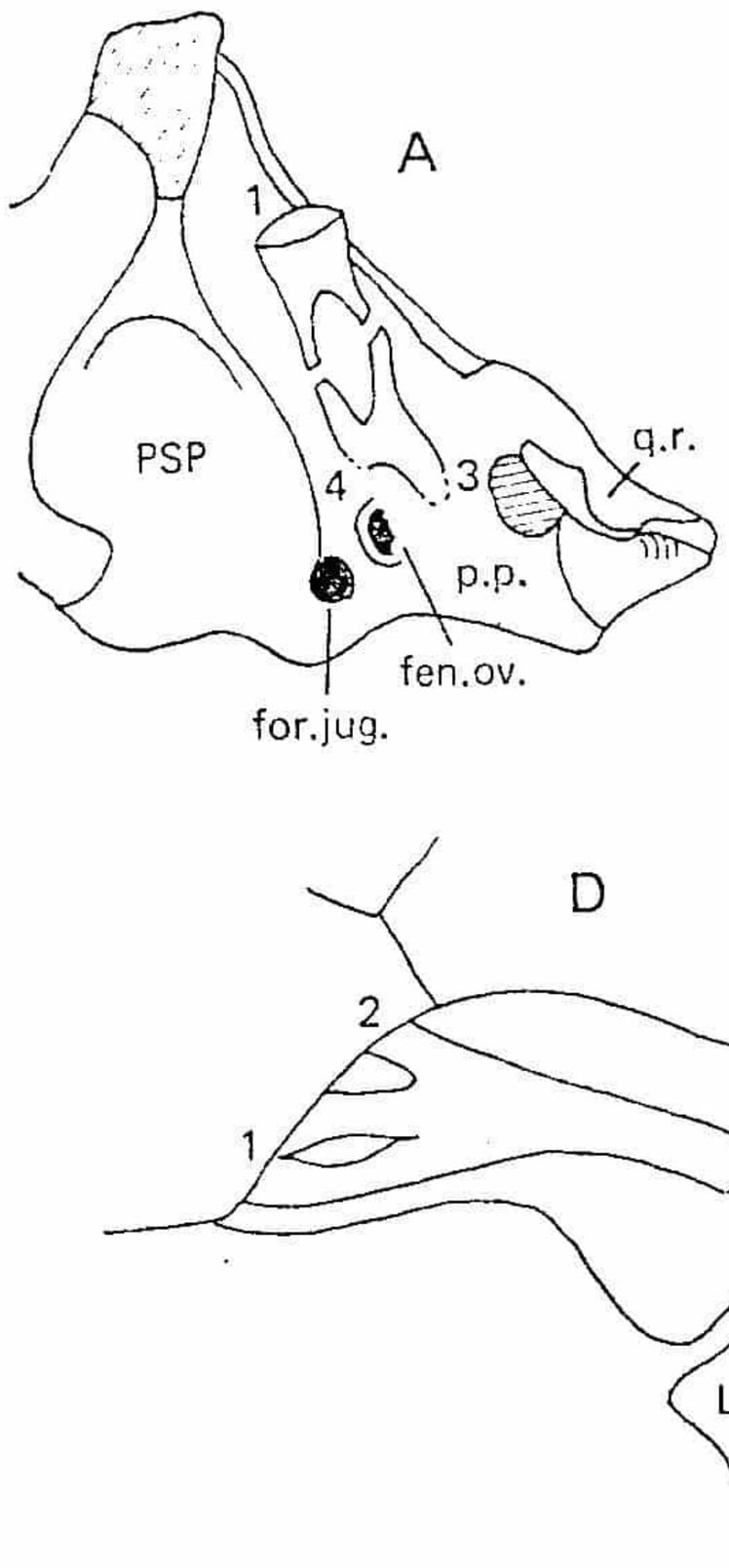
Later Westoll made the same check and others have also repeated it. None has expressed doubts on the matter. Allin takes a single plane sketch and without making any allowance for the fact that the proximal end of the stapes (inserted into the fenestra ovalis) and the supposed median end of the quadrate condyle must have lain in different planes, claims that the stapes would not fit as I had stated. His interpretation is not clear since many specimens have been shown with a stapes lying between the fenestra ovalis and only partly against the quadrate, and he illustrates one where the stapes appears to be jammed against the quadrate with no posterior overlap. Allin also comments on the fact that only in *Scalenodon* has a bony extra-stapes been found. This is true but it must be remembered that the extra-stapes in modern reptiles is cartilaginous. Furthermore it must be borne in mind that in the great majority of synapsid skulls one, or both, of the stapes is missing, having dropped out; that crushing is common and in consequence delicate processes are destroyed or hidden. To rely on a single specimen of a particular cynodont which is in contradiction to all other evidence on the matter is unwise.

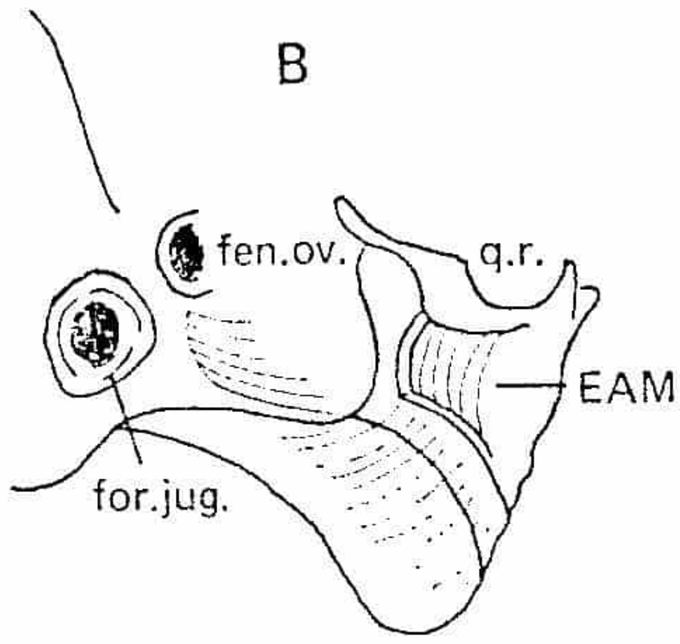
The next piece of the writer's research to impinge on Westoll's theory was an investigation of some small labyrinthodonts from the Lower Trias of South Africa (Parrington, 1948).

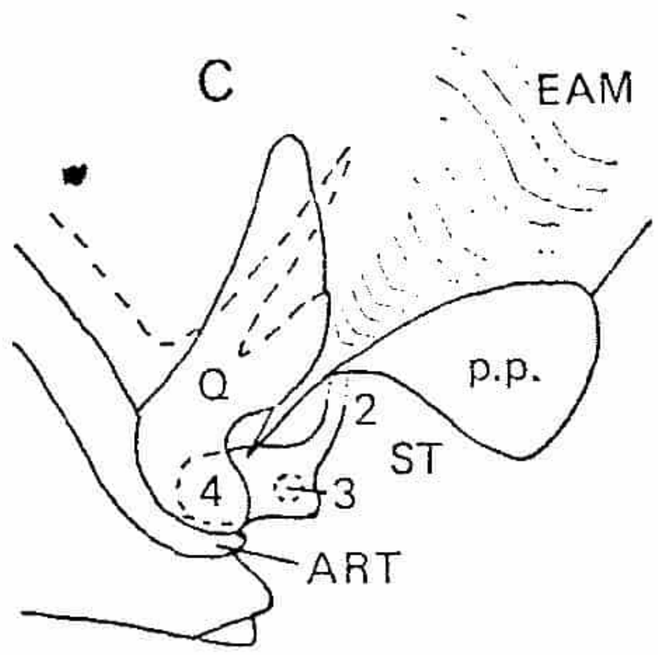
One specimen clearly belonged to a new genus (*Limnoiketes*). This, as do most labyrinthodont skulls, lacked the stapes. But two specimens of the long known form *Lydekkerina* had stapes in position or thereabouts. One, the posterior half of a skull, had the right stapes in place. Since the blackish bone contrasted with the red matrix it was decided to start on it. Careful preparation of the ventral surface of the stapes disclosed, rather more than halfway along the shaft, the presence of a small stub, about a millimetre in diameter and about a millimetre or less in length. This stub is just where a connection would be expected to occur according to the interpretation first put forward by Watson (1926) and accepted by Westoll, who illustrated the supposed continuation of the structure to the boss on the quadrate and to the hyoid. The preparation of the second specimen was more difficult, both the bone and the matrix being very pale and the bone soft. Again both stapes showed the stub. The interpretation of the labyrinthodont stapes put forward by Watson and illustrated by Westoll was fully justified, though the dorsal process does not seem to have parted far from the head of the bone (Parrington, 1948, fig. 3).

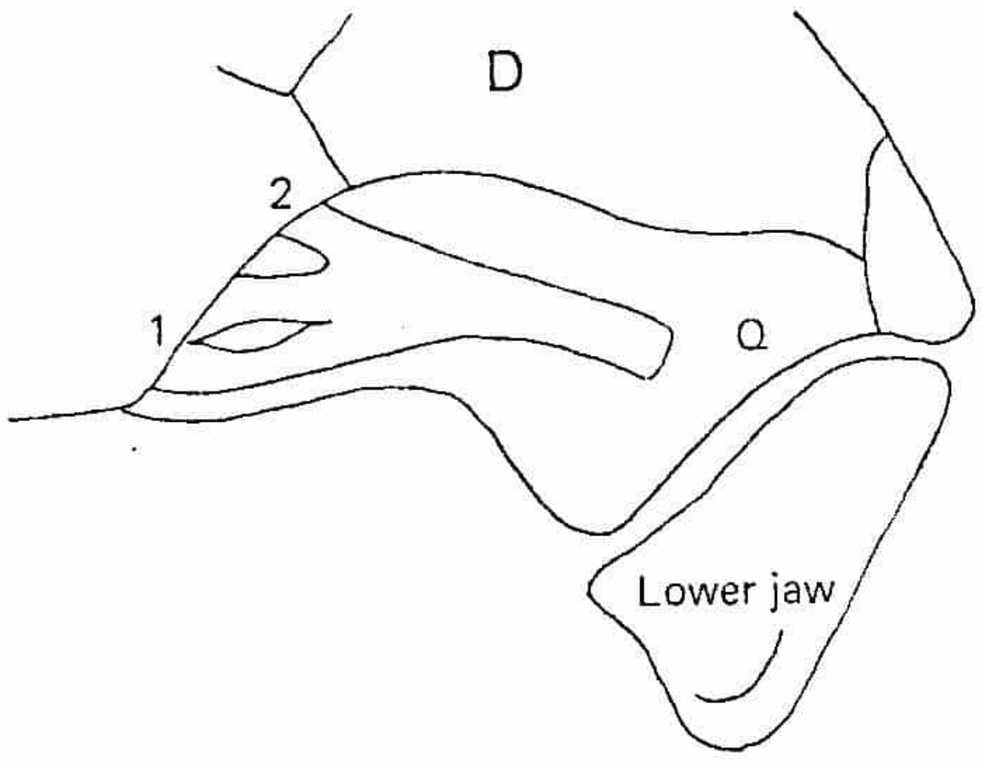
In 1955 still further evidence supporting Westoll's theory was obtained. In an account of the gorgonopsid *Scylacops* from East Africa a stapes, one of a pair, was described. This has a well developed dorsal process, which arises from its distal end and has an expanded foot. Furthermore, the proximal end is tapered and must have fitted some distance into the fenestra ovalis, and the distal end which projects laterally, is conical and not covered in perichondral bone. That both ends were finished in cartilage is clear.

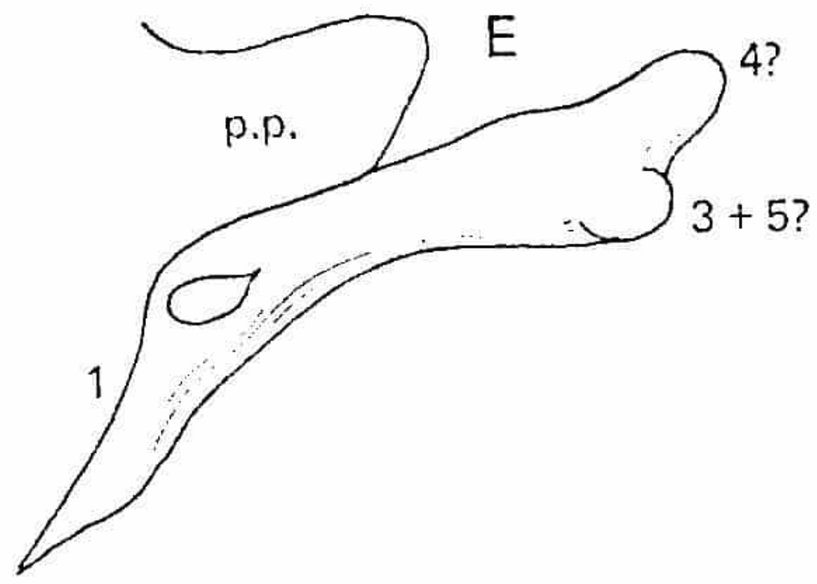
It seems as well to mention here the huge cynodont stapes which I figured in a discussion on the origin of monotremes (Parrington, 1974*a*). This is probably the stapes of a very large *Diademodon* which had been extracted from the rock by means of acid. Here there is a very wide process arising, not from the distal end, but from

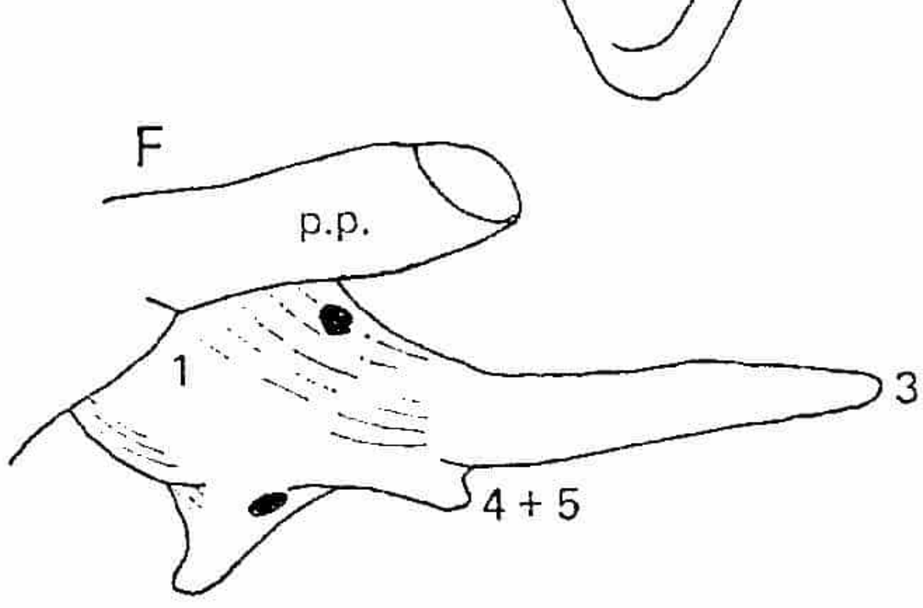


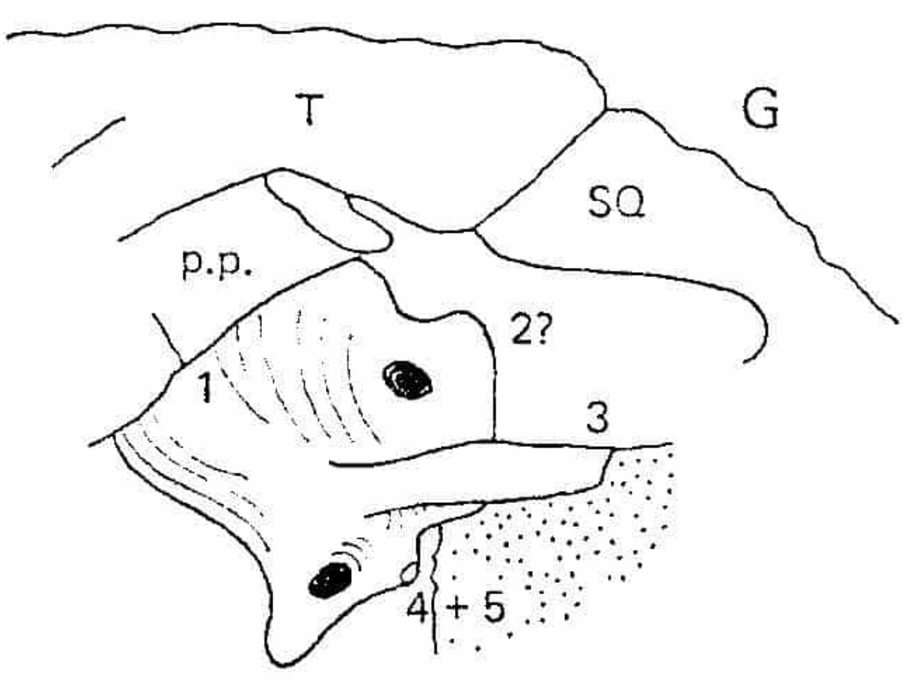


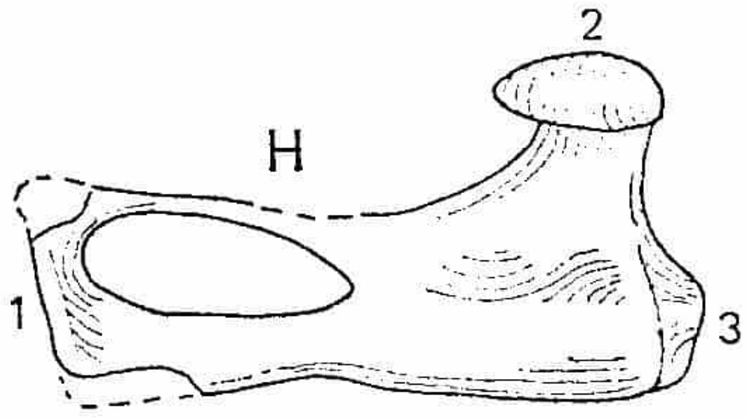












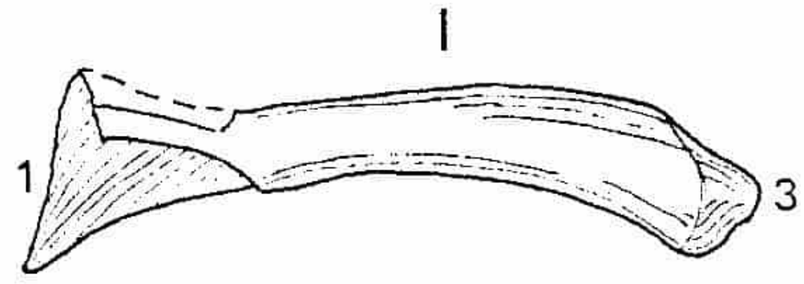


Fig. 3. The stapes of A, B, *Trirachodon* (*Scalenodon*); C, *Thrinaxodon*; D, E, *Captorhinus*; F, G, *Lydekkerina*; H, I, *Scylacops*. B shows the termination of the external auditory meatus, subsequently seen much better in other cynodonts. ART, articular; EAM, external auditory meatus; fen.ov., fenestra ovalis; for.jug., jugular foramen; p.p., paroccipital process; PSP, parasphenoid–basisphenoid complex; Q, quadrate; q.r., quadrate recess; SQ, squamosal; ST, stapes; T, tabular. (D after Westoll, the remainder after Parrington).

the central part of the shaft. It would seem likely that this development, which I interpret as a dorsal process, was wide and had a central position because of the huge size of the bone which was better supported that way. The enormous stapedial foramen could not possibly have been entirely filled by the stapedial artery and its great extent must have served to lighten the bone.

I feel that it is necessary to call attention again to the form of the stapes of *Captorhinus*. Here, while the dorsal process is still near to the footplate, as in the labyrinthodonts, the distal end is not a simple termination as is commonly figured, but there is an anteriorly directed process, which invites interpretation as the quadrate process, and, below it, a stub to which an extra-stapes could have been attached and from which a connection to the hyoid could have led (Parrington, 1955).

The discovery of these processes in *Lydekkerina*, *Captorhinus*, *Scylacops*, *Thrinaxodon* and *Scalenodon*, which were unknown at the time of Westoll's publications, convinced me that his theory was essentially correct.

It occurred to me, while pondering over recent work, that Broom had shown me, when I paid him a brief visit in Pretoria in 1942, a process in a therocephalian which he called an extra-stapes. This process was delicate and turned at right angles to the main shaft. While searching for a reference to this form, *Notalurops* (Broom, 1936), I came across another interesting matter. In 1937 Broom described *Galerhynchus rubigei* as the smallest gorgonopsid known and claimed that an extra-stapes extended behind the quadrate where he thought the tympanum must have been. It would now seem clear that the process in *Notalurops* was a dorsal process. I had overlooked these two references in my previous publications, I believe because they may have reached Cambridge just before or during the war, and in 1945 a small mountain of papers waited to be studied. Broom's descriptions of these processes thus anticipated my own discoveries but agree with them except for the fact that the unprepared extra-stapes of *Galerhynchus* could be too long and its preparation by modern methods is clearly desirable.

Allin prefers the evidence of a specimen of *Exaeretodon*, where the stapes abuts entirely against the quadrate, to all the evidence presented by me and others. In the great majority of specimens of synapsid and other reptiles one or both stapes have fallen out and must, therefore have been only loosely held. Baird (1970) reviewed the conditions in the ears of modern lizards and showed that they vary very widely. To rely on one cynodont is dangerous.

Many statements concerning the evolution of the middle ears of reptiles and mammals are very subjective – as they have to be. But Allin (1975) emphasizes the fact that the amphisbaenids "have neither a cavum tympani 'nor a' tympanic membrane" but low frequency aerial sound is heard well, being received by large scales overlying the mandible and transmitted by the extra-stapes. Again he points out that snakes also lack cavum tympani and ear drums yet are sensitive to air-borne sound of low frequency which is received by the general region of the head and even by the body with transmission via the lung. These recent discoveries are interesting in themselves, but Allin does not point out that the amphisbaenids are burrowers as were, it is generally maintained, the ancestors of the snakes (Bellairs, 1969). Such burrowers are

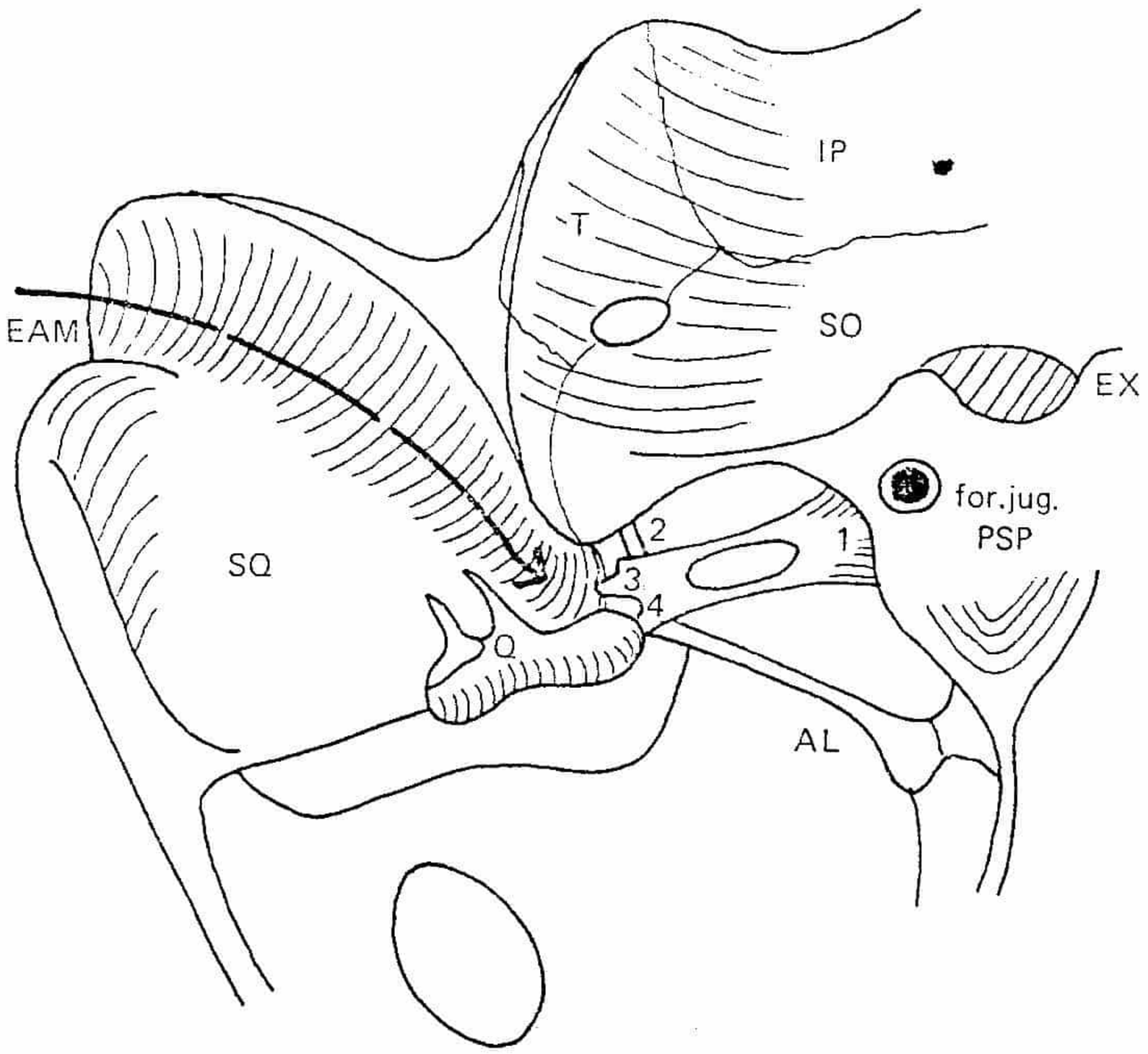


Fig. 4. Diagrammatic restoration of the cynodont middle and outer ears with the stapedial processes and abutments numbered as in the hyomandibular of *Eusthenopteron* (Fig. 2). AL, alisphenoid; EX, exoccipital; IP, interparietal; SO, supraoccipital. Other letters as before.

not subject to air-borne sound. The same applies to the Apoda. The loss of tympana, which are delicate, is understandable in such creatures.

A further comment remains to be made about the ability of the muscle-bound postdentary bones to transmit sounds of any reasonable strength. When Hotton (1959) published the results of his experiments which showed that there was an optimum size of tympanum for any given transmitter, I made estimations as well as I could about the mass of the stapes and the size of the tympana that I had conjectured in both gorgonopsids and cynodonts. It was very satisfying to find that these related reasonably closely to the optimum ratios found by Hotton. A manuscript was written to this effect (and calling attention to the huge cynodont stapes described by me in 1974*a*) but it was never published because at the time it appeared to be 'flogging a dead horse'. The background data are in print and available to anyone who is interested in them. It is of especial interest to examine the proposed arrangement put forward by Watson (1951), for the angular-held tympanum is vastly too large to activate the stapes efficiently. Meanwhile it is worth quoting Hotton (p. 112): "It is very probable that these tympana postulated on morphological grounds by Parrington and by Westoll are entirely large enough to have been able to actuate the stapes with which they are in association" (Fig. 4).

If, as I believe, the quadrates of typical theriodonts were mobile to a greater or

lesser degree, and if, as seems very probable, the dorsal process of the stapes served to prevent its distal end from dropping, it seems very unlikely that the tympanum could have been in part supported by the quadrate as I at one time believed. The conclusion that it was supported by the squamosal which lies behind the dorsal process of the quadrate is more likely.

IV. THE EXTERNAL AUDITORY MEATUS

In 1910 Gregory advanced the view that the groove in the back of the zygomatic arch in cynodonts housed the external auditory meatus, a conclusion resulting from the comparison of cynodont skulls with that of the marsupial thylacine wolf. Watson hailed this identification as excellent (1911) and it has been universally accepted until recently (Allin, 1975).

What was troublesome about this interpretation was that it did not seem to conform to Watson's view that in synapsid reptiles the tympanum was already held by the angular with its reflected lamina. If the tympanum was held by the angular it was already external and so needed no long external meatus. It led to the extraordinary illustration published by Watson in his Silliman lectures (1951) which shows the external auditory meatus reaching the tympanum on its inner side.

The discovery, made in 1946, when I was examining the imperfect remains of *Scalenodon angustifrons* (at the time wrongly identified as *Trirachodon*) of what appeared to be the termination of the bony housing for the external auditory meatus was important. This structure lay behind the position of the quadrate (which was missing) and was slightly expanded terminally. This, to me, strongly argued that the reptilian tympanum lay, where it would be expected to lie, behind the quadrate and at the end of the external auditory meatus which was near the distal end of the stapes in forms where that bone is known.

Since it now appeared fairly certain that Gregory's view was right, it became necessary to account for the origin of the long external auditory meatus. This I tried to do in 1955. I suggested that if a captorhinomorph reptile had a tympanum, and the loss of the labyrinthodont otic notch is no evidence of the loss of the tympanum, as anyone who has seen the skull of the South African lizard *Zonurus*, for example, will know, it must have been held behind the quadrate. This was the position it occupied in phyllospondylous (larval) labyrinthodonts and now occupies in living reptiles (Parrington, 1959). But as I showed in 1955 (fig. 14) the quadrate in the pelycosaur *Dimetrodon* had been brought down a long way below the position it occupied in *Captorhinus* which was just below the tabular and the end of the paroccipital process. This point is very conveniently illustrated by Panchen (1972) in his fig. 6 where the occiputs of *Eothyris* (a captorhinomorph), *Ophiacodon* (a primitive pelycosaur) and *Dimetrodon* are all illustrated (see also his fig. 2). I suggested that if a shallow external auditory meatus existed in captorhinomorphs, as might well occur, it would have to lengthen if it was to function in pelycosaurs, and I illustrated its probable course in *Dimetrodon*. It was very reassuring to have this idea confirmed when I visited Princeton in 1964 and Dr D. Baird showed me the cast of a beautifully preserved skull of *Dimetrodon* which has a semi-circular cavity, which would enclose almost half a forefinger, just

about where I had suggested the external auditory meatus would have left the skull. This specimen, collected by the Romers, is in the Harvard Museum of Comparative Zoology.

Gregory's interpretation was supported by the presence of a deep groove in the back of the skull of the dinocephalian *Ulemosaurus*, and a slight hollowing in the zygomatic arches of gorgonopsids. But it received its most convincing support from Watson. When he last visited Cambridge, before fully retiring, he brought with him a huge skull of the cynodont *Diademodon* and here, on one side, the external auditory meatus tapered and reached down to the level of the lower surface of the paroccipital process and then turned abruptly inwards towards the fenestra ovalis to terminate near the position where the stapes would have been expected to have had its postero-distal end. It completely confirmed the conclusion I had reached in 1946 when I studied the rather poorly preserved remains of *Scalenodon*. I intended to describe and illustrate this specimen when Watson fully retired from research and generously gave his collection of fossils to the Museum of Zoology at Cambridge. But when I examined the collection I could not find the specimen. After some thought it occurred to me that the number on some skull fragments listed in Watson's register as *Diademodon* might be parts of a once good skull. I referred to a paper by Kermack (1963) wherein there is a photograph of the brain case of the cynodont *Diademodon*. The numbers are the same. It seems that the superb specimen showing the course of the external auditory meatus very perfectly on one side, had been broken up. However, I wrote to Dr A. R. I. Cruickshank in Johannesburg asking him if he had any material which would show this abrupt inturning of the bony external auditory meatus. Cruickshank kindly sent me a set of stereophotographs of a series of theriodonts showing the various developments of the external auditory meatus, one of a large *Diademodon* showing the abrupt inturning of the meatus to perfection.

Allin's (1975) interpretation of the groove in the squamosal leads to most curious difficulties. First it must be supposed that the depressor mandibuli muscle left its area of origin on the occiput and moved onto the zygomatic arch. How, when and why did this change take place? Next the origin of the therian digastric muscle must be accounted for. The simplest explanation (in fact the only one known to me) is that the insertion of the depressor mandibuli muscle on the retroarticular process was led first downwards, then forwards and finally upwards until it reached the position of the mylohyoid muscles and had only to join one by a ligament to form that curious therian muscle, the digastric muscle (Parrington, 1955, 1974*a*). The reason for the downwards and later forwards movement of the process has already been explained functionally (Parrington, 1955). True it has been shown by Crompton, Cook, Hiiemae & Thexton (1975) that it is not an important one but at least the great majority of the Theria have a digastric muscle and its origin must be explained.

If Allin's idea is accepted, either the depressor muscle must have moved back onto the occiput and formed the posterior belly of the digastric, or it must have been lost and an entirely new muscle must have been developed from the same muscle block, innervated by the same nerve, the facial (VIIth) and by some quite unknown means become attached to a mylohyoid muscle, innervated by a branch of the trigeminal

(Vth) nerve. Finally it is then necessary to explain how, when and why the mammals developed their characteristic and seemingly unnecessary long external auditory meatus, unnecessary because the angular bone was always external.

Allin's published views, before they can be accepted, introduce a number of problems which must be solved. However, I understand (personal communication) that he no longer holds his views so strongly.

I have received from A. W. Crompton a page from a forthcoming publication together with a figure. To deal with the figure first. This shows the ear region of two cynodonts and two mammals. The illustration of the ear region of the cynodont *Probainognathus*, as drawn, denies that the supposed external auditory meatus functioned as such because of the relations of the quadrate and stapes to it. When (1946) I first described the quadrate complex of the cynodont *Thrinaxodon* I pointed out that if the quadrate slipped down a little when the jaw was opened and only returned to its fully dorsal position when the full power of biting was exerted then two things followed. Because the dorsal process of the quadrate was somewhat curved the teeth would move slightly backwards at the last moment and this would account for the propalinal wear found in gomphodont cynodonts. Furthermore, it would explain the value of the backwardly directed flanges on both the quadrate and quadratojugal which, fitting into slots in the squamosal, would prevent these bones rising too high when full biting power was exerted. As illustrated, the quadrate complex of *Probainognathus* is in what I suggested was the lowered position with regard to the external auditory meatus. Drawn with the complex pushed upwards a little, this cynodont would agree with other cynodonts. It is worth noting that, as drawn, the quadrate is about in line with the middle of the squamoso-surangular glenoid. But in the more primitive *Thrinaxodon* the quadrate condyle is in line with, or behind, the area of a connection to the surangular as it is behind the glenoid in the mammal *Megazostrodon*. It is noteworthy also that when Crompton (1972) described the evolution of this accessory hinge he showed that the new structure was largely in front of the quadrate in the cynodonts *Trirachodon* (fig. 4 B), *Diademodon* (fig. 5 D) and *Probelesodon* (fig. 8 B). Here again a single species (or specimen?) has been used for a generalization. *Probainognathus* has been well illustrated in this work by three stereophotographs of two specimens which readers can consult (plate IV).

With regard to the typewritten sheet, it is difficult to judge a matter when one starts *in medias res* and it would appear that this is so since the first sentence starts "An alternative possibility....". But certain comments are needed. First, the statement is made that because the theropsids and sauropsids had a common stock no later than the middle Carboniferous it is possible than the cynodonts had a detrahens muscle like the monotremes and, it is implied, no depressor mandibuli muscles. This does not account for the fact that modern amphibia have depressor mandibuli muscles as did labyrinthodonts according to Watson (1926) and Panchen (1964, 1977) for example. Nor does it explain how the non-cynodont synapsids opened their jaws. This follows because the detrahens muscle is a derivative of the masseter muscle which, Crompton believes (following Barghusen), did not arise until the cynodonts evolved. (I have never held that the detrahens muscle is a neomorph, as I understand that word.)

Recently Kemp (1978) has commented on the fact that the external auditory meatus is more pronounced in the later cynodonts *Cynognathus* and *Diademodon* than in the earlier forms *Procynosuchus* and *Thrinaxodon*. But this is surely a matter of size, the two latter forms being much smaller and so having proportionately larger brains and brain cases and such parts as the paroccipital processes are in the larger forms proportionately larger as was the stapes which keeps pace with this process (Watson, 1931). As he pointed out this was one reason why the mammalian ancestor must have been a small animal.

Finally Dr R. Presley informs me (personal communication) that his study of the monotremes convinces him of the correctness of Gregory's interpretation of the external auditory meatus though he would place the tympanum lower than I do. Eventually this must happen since the skin lateral to the angular became the tympanum. But I can see no position where this could have happened in cynodonts and doubt if it happened until the squamosodentary hinge took over the main stress of the hinge of the lower jaw in such an animal as *Eozostrodon*.

V. THE LOWER JAW AND ITS MUSCULATURE

It seems to me that many of the current re-interpretations and difficulties concerning the origin of the mammalian middle and outer ears stem from Barghusen's (1968) denial of my suggestion that the reflected lamina of the angular of the sphenacodont pelycosaurs and their descendants served to give insertion to that essentially mammalian muscle, the masseter. The reflected lamina of the angular is found only in the reptilian ancestors of the mammals and the full development of the outer component of the adductor mass – the masseter – is found only in mammals. I am not aware of any satisfactory alternative function which has been advanced for this lamina.

The great interest which is engendered by the various studies of the cynodont lower jaw caused me to read the work of Adams (1919). A student of W. K. Gregory's famous school, he wrote on the phylogeny of jaw muscles, first making himself familiar with a wide range of living vertebrates. He used the knowledge thus acquired to project muscle systems for a wide range of extinct forms using osteological evidence where it could be found. I formed a high opinion of this work, but it is seldom referred to today.

In 1934 I pointed out that the cynodont lower jaw could be regarded as a lever on which the temporalis muscles pulled upwards and backwards and the pterygoideus muscles pulled upwards and forwards (and today I would add also the masseter – see below) and that the anterior and posterior components of these forces might just about cancel each other out leaving largely the vertical forces. It is elementary mechanics that the further forward this biting force was situated the greater would be the power of the bite and the less the force which would be wasted thrusting against the quadrate hinge. The distribution of the biting forces would be in accordance with the inverse ratio of the points of reaction from the hinge and the point of the bite. I have taught this view for many years and Crompton has illustrated it in a series of papers (e.g. Crompton, 1963; Crompton & Parker, 1978). Crompton has now aban-

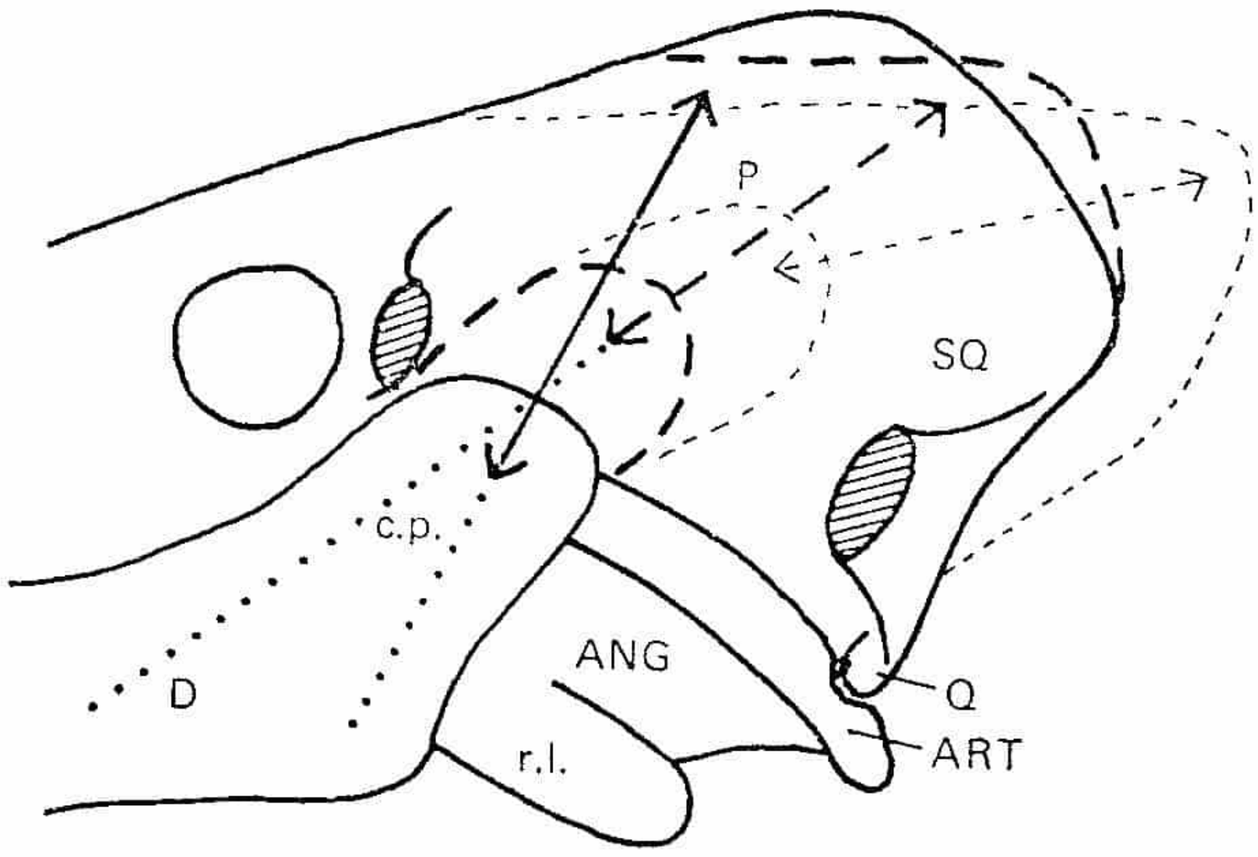


Fig. 5. Diagrammatic representation of the action of the cynodont coronoid process whereby without losing leverage the thrust of the temporalis muscle acts increasingly further forward while the height of the cranium can be lessened. The angle of attack being reduced the vertical component becomes less. c.p., coronoid process; P, parietal. Other letters as before.

doned the view that the masseter muscle was attached to the reflected lamina of the angular (see also Kemp, 1969, 1978) but an important point, it appears, has been overlooked in understanding, if not in illustration. The development of the coronoid process of the dentary was the development of a bell-crank lever which, so long as it did not allow the line of action of the temporalis muscle to reduce its distance from the condyle (and so lose leverage), served to transfer more of the bite forward onto the row of teeth (Fig. 5). Being trapped behind the orbit it cannot migrate forward to achieve greater leverage, as did the masseter muscle which can move so far anteriorly that its action on the hindmost teeth becomes that of a pair of nutcrackers and actually tends to pull the hinge apart rather than compress it. The larger the dentary grows the greater the area for attachment of adductor muscles and, eventually the lower jaw becomes stronger by being composed of only a single bone. But the lower angle of attack which results from this modification would reduce the vertical component. However the later and larger cynodonts, having proportionally smaller brain cases, had room for larger temporalis muscles.

The supposition that the enlargement of the dentary served to lighten the postdentary bones and so fit them better for the conduction of air-borne sound is one I find difficult to appreciate. It presupposes that the very large and muscle-bound postdentary bones of the eotheriodonts and the large Permian theriodonts actually conducted air-borne sound, a supposition I find difficult to accept.

It is worth comparing the dentary of the procynosuchids, where the coronoid process is short and directed upwards and backwards towards the crest of the noticeably high cranium, with the condition in *Thrinaxodon* where the process is larger and somewhat recurved and the cranium less high, and that with the condition in later cynodonts. Best of all, if the reader is to understand my views, some members of the modern carnivore family *Mustelidae* should be examined. Here the coronoid process is about vertical and the cranium low and long, as befits animals which hunt

their prey in tunnels and nooks and crannies as do ferrets, stoats and weasels. Here the cranium has been extended far behind the hinge for the dentary and the temporalis muscle must act almost horizontally when the jaws are closed. I find it very hard to accept the view that the increase in size of the dentary "involved selection for auditory acuity rather than an evolutionary development in mastication alone" (Crompton & Jenkins, in press). That the early and often massive postdentary bones of the early theriodonts were muscle-bound seems agreed by everybody.

In 1955 I discussed the six interpretations which had been put forward to account for the reflected lamina of the angular bone, that very curious feature of the sphenacodont pelycosaurs and their descendants the Therapsida, and called attention to the objections which had been raised against all of them. I then suggested that this essentially mammalian-ancestral feature might well be associated with that essentially mammalian muscle, the masseter. I pointed out that the thickenings found on the reflected lamina would strengthen it against any muscle-induced lateral strain and, also, that in the gorgonopsids *Dixeya* and *Scylacops* the zygomatic arch was thickened at its anterior end where it meets the maxilla and that I could find no alternative interpretation except that this was a strengthening which provided for the area of origin of the masseter muscle. This thickening is particularly well shown in the form I have called *Cephalicustriodes* (Parrington, 1974*b*). When demonstrated to the late Professor D. M. S. Watson he exclaimed "I *wondered* what that was for". I have had little access to large Therocephalia.

Barghusen has a series of objections to my interpretation of the reflected lamina of the angular. I find his writing difficult to follow partly, perhaps, because he modifies his views somewhat in an addendum. In his discussion of the Captorhinomorpha, the ancestors of the pelycosaurs, Barghusen lays great emphasis on *Captorhinus* itself, claiming rightly that the ornament on the outer side of the mandible posteriorly precludes the assumption of adductor muscles being present on the outer surface and so he claims that the suggestion that the masseter muscle arose in captorhinomorphs is not, therefore, tenable. But *Captorhinus* is one of the latest and most specialized of the captorhinomorphs and the earlier forms *Protorothyris* (Specimens 2148 and 2149 in the Museum of Comparative Zoology at Harvard University) and also the type specimen of *Romeria* in the same Museum show the uppermost part of the hind region of their mandible to be smooth. The adductor muscle could well be attached in this region as in, for example, *Sphenodon* (see Adams, 1919). In view of the fact that both captorhinomorphs and pelycosaurs are known from far down in the Carboniferous (L. Pennsylvanian) the use of the specialized *Captorhinus* is unfortunate. But there is good reason for doubting my 1955 conclusion. Only sphenacodont pelycosaurs have a reflected lamina and, unless the pelycosaurs were diphyletic, the structure must be held to have evolved within that group.

Next Barghusen holds that the surface of the reflected lamina of *Dimetrodon* has the same sort of surface as the dorsally situated dermal bones and, therefore, it was probably covered only by skin, and he leaves its function unexplained. Also he likens these surfaces to those of the Green Turtle, *Chelone midas* which have fine grooves on them carrying fine blood vessels and nerves. The grooves in *Chelone* radiate from their

growth centres. I can find nothing like them in the single skull of *Dimetrodon* available to me but here the reflected lamina has been largely broken away.

Examination of the dentary of a well-preserved specimen of *Thrinaxodon liorhinus* shows that the bone forming the fossa for (it is agreed) the temporalis muscle is finely striated along the line of the fossa but the thickened sides are not so striated. The striations from the fossa are continued along the centre of the horizontal shaft of the bone as far forward as the first postcanine tooth. Nobody has claimed muscles along this part of the dentary.

I am authorized by Professor A. Bellairs to say that in reptiles he is unable to distinguish between bone which is covered only by skin from bone giving rise to a muscle unless, of course, there is a process or fossa for muscle attachment.

Next, Barghusen holds that the ribbing, to me strengthening, on the reflected laminae of the Theriodonta (and *Bauria* itself) is not suitable to resist the pull of an antero-dorsally directed muscle but is suitable to resist an inter-mandibularis muscle. This is a matter of opinion and one with which I am unable to agree, particularly because others also agree with me. These radiating ribs typical of large theriodonts (small animals do not show them) are ideally suited to resist any lateral pull exerted by a masseter muscle just as the ribs of a fan resist the air when it is waved.

Again the mistake is made of arguing that because the tensor tympani muscle is innervated by the trigeminal nerve and not the facial and is attached to the manubrium of the malleus it suggests an origin from the detrahens muscle. The tensor tympani muscle is not attached to more than the very base of the manubrium of the malleus (this has all be expounded by Parrington, 1978) whereas if the depressor mandibuli had retained its connection with the malleus (articular) it would be at the *end* of the manubrium as it was at the *end* of the retroarticular process of the articular. Relics of the depressor muscle are to be found not only in the posterior belly of the digastric muscle but also in the stapedial muscle and the tensor palati.

Those who are inclined to follow Edgeworth (1935) should bear in mind that he believed in the theory of 'Recapitulation' and used it in his interpretations. This accounts for his difficult and personal nomenclature. And, of course, he had no knowledge of the great variation of form of the retro-articular processes in the Pelycosauria, the Theriodontia and the Dicynodontia which has to be explained. I have sometimes tried to picture the not insignificant posterior belly of the digastric muscle attached for a time to the now minute malleus (articular) to show that "Ontogeny recapitulates Phylogeny". I have been unable to make that picture.

Finally one theriodont which might conceivably have used its fantastically large reflected lamina as a receptor of air-borne sound is *Acalaporhinus angulor rugatus* Boonstra (1953), and some of its allies. This form has not been discussed in recent works.

VI. CONCLUSIONS

1. It is emphasized that there is substantial palaeontological evidence supporting Westoll's theory equating five attachments or points of contact of the crossopterygian hyomandibular bone with points of attachment or contacts in the tetrapod stapes.

2. The suggestion that the groove in the back of the zygomatic arch in cynodonts served in fact to house the depressor mandibuli muscle results in unanswerable questions as to how, when and why the transference from the occiput took place; why an external auditory meatus of considerable length evolved in mammals if the conduction of sound was already via the postdentary bones which are external in early therapsids; and requires the view that the muscle-bound post-dentary bones of the therapsids were conductors of sound.

3. It is pointed out that the development of the coronoid process of the dentary acted as a bell-crank lever to transfer the biting power of the temporalis muscles forward onto the dentition. It is claimed that the objections to the view that the reflected lamina of the angular carried the masseter muscle appear to be invalid. It is not possible to judge whether a bone was covered only by skin or supported a muscle unless a process or fossa is present. Not only is the reflected lamina left unaccounted for in modern writings, but so also is the strengthening of the zygomatic arch in gorgonopsids, some large therocephalia, and *Bauria*.

4. The various modifications of the retroarticular process found among the Pelycosauria and the Therapsida are explicable only in terms of a depressor mandibuli muscle changing according to the slope of the occiput and the development of canine teeth which require a greater rather than a smaller gape. The final modification found in some large cynodonts led the tendon of the depressor mandibuli muscle close to the region of the mylohyoid muscle when the digastric muscle could be formed by joining the depressor mandibuli muscle to a slip of the trigeminal-innervated mylohyoid muscle.

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